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Animal Behavior: The Orphan Rebellion

After their queen has left with a swarm, orphaned larvae exhibiting rebel traits emerge in honeybee colonies. As adults, these orphans have reduced food glands to feed the colony's larvae and more developed ovaries to selfishly reproduce their own offspring.

James C. Nieh

Honey bees (*Apis mellifera*) are social insects and live in colonies that reproduce through fission. Approximately half of the colony departs in a swarm with the old queen, leaving her daughters behind to raise a new queen [1]. Thus, the colony can be temporarily queenless after their original queen has left with a swarm. The colony continues by raising a new queen and daughters that are kin, but may be less than kind. In this issue of *Current Biology*, Woyciechowski and Kuszewska [2] show that this period of queenlessness affects female larval development. Female larvae typically develop into workers that act as nurse bees while they are young. Their hypopharyngeal glands secrete a protein-rich brood food that is fed to all larvae [3]. Unlike other daughters who focus on tending their sisters, 'orphans' grow up with enlarged ovaries and reduced hypopharyngeal glands [2]. In fact, these orphans have the physical characteristics of 'rebels' who reproduce their own offspring, a surprising finding because such selfish reproduction is very rare under normal conditions [4].

The cooperative breakdown demonstrated by Woyciechowski and Kuszewska [2] illustrates the power of kin selection theory to generate productive hypotheses based upon the honey bee sex determination system and resulting kinship asymmetries. Honey bees have a haplo-diploid sex determination system, whereby fertilized diploid eggs will develop into females and unfertilized haploid eggs will develop into males (Figure 1). All workers are female. Unfertilized workers can produce sons, but normally do not for a variety of reasons. Queen pheromone suppresses worker ovarian development [5], and workers normally police the colony and remove eggs laid by other workers [6]. Most importantly, workers are more closely related to their brothers (the queen's sons) than they would be to their own male offspring. Workers share, on average, 25% of their genes with their brothers and only 14% of their genes with worker-produced sons, assuming a queen that has mated on average with males from 17 different patrilines [2].

However, a shift in relatedness occurs when a colony splits during swarming: the old queen leaves with the swarm and the colony raises one of her daughters to become the new queen. As a result, the new queen's offspring are less related to the original daughters that remain in the colony as workers. These original daughters face a choice: reproduce and raise their own offspring (sons) or rear the less related offspring of the new queen (nieces and nephews). Kin selection theory predicts that some will choose the rebel path [7].

Many Roads to Rebellion

In a normal honey bee colony with an active egg-laying queen, eggs laid by workers are rare. The presence of queen pheromone decreases ovarian development in adult workers [5]. Only one in 10,000 workers has a developed egg in her ovaries and 85% of worker-laid eggs are removed within one day through worker policing [4,8]. In a few cases, anarchic colonies have been discovered containing workers that lay male eggs which successfully evade worker policing [9]. There is a strong genetic component to this anarchic behavior. Genetics also underlie the ability of the Cape honey bee (*A. m. capensis*) to use thelytokous parthenogenesis. In this case, unmated females can produce female eggs, giving rise to 10.5% of workers and 0.48% of drones in a queenright colony [10]. Woyciechowski and Kuszewska [2] explore a different phenomenon, because they show that the absence of a queen during the larval development of workers creates long-lasting physiological changes that persist in a queenright situation. Unlike anarchistic lineages or the Cape honey bee, these 'rebels' do not originate in a queenright colony and are not based upon inherited genetic differences.

Delving into the Rebellion

The authors [1] conducted two experiments to determine if larvae would respond to the decrease in queen pheromone by developing into more queen-like adults. The first experiment used naturally swarming honey bee colonies and the second used split colonies in which the queen was removed. In the first stage of each experiment, larvae developed in a colony with or without a queen. Larvae that developed in the presence of the queen had been fed while the queen was present and were, therefore, exposed to queen pheromone, its breakdown products, or a downstream effect of queen pheromone. In the second stage, these potential rebels were returned to their natal colonies, half of which had no queen.

Being reared in a queenless colony did not affect larval body mass. However, these orphan larvae developed into workers with more ovarioles and

Figure 1. Droning out.

Worker honey bees are crowded around a sealed drone cell. Drones are normally produced by the queen, but in rare cases can be produced by workers. (Photo: Daren Eiri.)

a greater potential for egg laying. They also had enlarged mandibular glands, the source of queen pheromone. Young workers normally act as nurse bees and have well developed hypopharyngeal glands to secrete brood food. In contrast, orphan larvae emerged as workers with smaller hypopharyngeal glands. They had the physical traits of rebels: bees set to reproduce, not to nurse. These rebels retained their distinctive differences even after being returned to a queenright colony. As adults, after 15 days, these rebel workers continued to display increased ovary activation, smaller hypopharyngeal glands and larger mandibular glands as compared to controls.

Thus, the reproductive physiology of the rebels, attained during larval development in a queenless colony, can have persistent effects even after a new queen emerges. This raises several new questions. Will worker policing intensify while the old daughters are around, and what proportion of worker eggs will escape the police? Even if the rebels do not lay eggs, other aspects of their biology may change. For one, they may feed larvae less often than non-rebels. They may also live longer. Workers that are less involved in brood rearing live longer than those that do [11], and ovarian development is correlated with longevity [12].

This last possibility casts a different light on the situation, a potentially adaptive angle. The detriment of rebel-laid eggs could be offset by enhanced worker longevity at a delicate point in colony life, a gap in egg production before the new queen is ready. The new queen requires time to mate and begin laying eggs. In some cases, this may not even happen because queen mating can be perilous: if the virgin queen does not return from her mating flights and the colony cannot re-queen itself, adult workers develop their ovaries and lay male eggs [13]. This last gasp of effort spreads the colony's genes through male production. Rebels, still daughters of the queen, have the advantage of being primed for such a situation, providing for all the twists of outrageous fortune. The future of the story of the orphan rebels will be fascinating to watch.

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Cell Polarity: Centrosomes Release Signals for Polarization

New findings reveal that, in *Caenorhabditis elegans* embryos, the centrosome provides signals that induce cell polarization, independently of its function as the microtubule-organizing center.

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The centrosome has been attracting the interest of biologists for over 100 years, but it is still an enigmatic organelle. In most cells, centrosomes are the major microtubule-organizing center (MTOC), and their best-known role is to organize mitotic spindles.